

TEMPERATURE EFFECTS ON OXYGEN CONSUMPTION BY  
*HELIOMA* FROM A REACTOR COOLING RESERVOIR

by

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ABSTRACT

Oxygen consumption by two species of *Helisoma* distributed differentially in a reactor cooling reservoir has been measured at field temperatures and at 5, 10, and 15°C above field temperatures. *H. trivolvis* from Warm Station and Cold Station areas showed a significant seasonal response at field temperatures but showed reduction of dependence of oxygen consumption on temperature at the elevated temperatures. *H. anceps*, cold species, exhibited a significantly stronger response to seasonal variations at field temperatures than *H. trivolvis*.

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## INTRODUCTION

The littoral zone plays a major role in the productivity of temperate lakes (Brown and Austin 1973, Wetzel 1975). Energy flow through a lake system depends heavily upon the function of the littoral zone organisms. Sedentary organisms of this zone are most likely to be exposed to thermal discharges which may float on ambient temperature waters and dominate the shallow edge zones receiving the discharges.

Temperature elevation associated with thermal effluents is expected to result in altered metabolism, especially in ectotherms (Wieser 1973, Prosser 1976). Patterns of metabolic response range from near-perfect acclimation, resulting in temperature-independent metabolism, to virtually no acclimation resulting in temperature-dependent metabolism (Precht, et al. 1973). The response pattern which will occur in a particular organism is not generally predictable. Since response patterns have been defined primarily from laboratory observations using constant temperatures, applicability of the patterns to field situations is dubious.

This paper reports the results of measurements of oxygen consumption of orb snails (*Helisoma*) from a reactor-cooling lake. The measurements were made at field temperatures and at temperatures above field temperatures for field-acclimatized snails. Objectives were to determine the extent to which the metabolic requirements of these organisms might be altered by life at the slightly higher habitat temperatures produced by the thermal effluent and to determine whether

the response of these animals to acute temperature elevation differed in relation to their acclimatization history. For the ambient temperature station we sought to compare the responses of two species of *Helisoma* living in the lake.

### The Experimental Organisms

Two species of orb snail were collected from Par Pond, a reactor-cooling reservoir in South Carolina. A systematic sampling of littoral areas (Figure 1) revealed that *H. trivolvis* is copiously distributed throughout the reservoir including the region subjected to temperatures above ambient. *H. anceps* is as abundant as *H. trivolvis* in ambient-temperature water but is virtually absent from the heated water.

The geographic distribution of *H. anceps* widely overlaps that of *H. trivolvis*, which is one of the most widely distributed of freshwater pulmonates in North America (Pennak 1953, Ward and Whipple 1959, van der Schalie and Berry 1973). The two species are frequently found in the same lake. Temperature is thought to be among the chief factors determining the worldwide distribution of pulmonates (Walter 1906) and the distribution within a single habitat (Kirkland 1900, Hunter 1953, Boray 1964). The local pattern of distribution in Par Pond appears to be consistent with the report that *H. anceps* has lower temperature optima for growth, reproduction, and survivorship than *H. trivolvis* (van der Schalie and Berry 1973). However, because the difference between temperature optima for the two species is small and

because the temperature of both ambient (Cold Station) and treated (Warm Station) water are within the tolerance ranges of both species, more subtle factors (e.g. competition and metabolic effects) must be operating to exclude *H. anceps* from the warmer areas of Par Pond.

### Study Site

Par Pond was constructed in 1958 to provide cooling water for the heat exchangers of two nuclear-production reactors. Currently, the reservoir serves only one of these reactors. Savannah River water is added to the effluent from the reactor (to compensate for evaporative losses from Par Pond). A thermal gradient is created where the pond-river water mixture enters the middle arm (Figure 1) of Par Pond. The temperatures of the rest of the reservoir are comparable to those of other southeastern coastal plain lakes (Tilly 1973). Periods of stratification are from April to October. The reservoir receives natural inflow from a parent creek at its extreme northern tip and from local drainage and seepage. Additional limnological features and nutrient and primary productivity cycles have been reported by Marshall and LeRoy (1971), Marshall and Tilly (1971), Tilly (1973), Lewis (1974), and Grace and Tilly (1976).

Two principal sampling stations were established: one located near the discharge and one in ambient temperature waters (Figure 1). The warmer station had an annual temperature range of 13 to 36°C with an average of  $24 \pm 1^\circ\text{C}$ .<sup>\*</sup> The diurnal temperature fluctuation was

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<sup>\*</sup> Here and elsewhere in this paper, the  $\pm$  symbol indicates one standard error.

approximately 3.0°C in the summer and 2.4°C in the winter. The annual temperature range of the colder station was 11 to 31°C with an average of  $21 \pm 1^\circ\text{C}$ . The diurnal fluctuation was approximately 1.5°C in the summer and 1.4°C in the winter. The average temperature difference between the two stations was about 5.7°C during the summer and 2.5°C during the winter.

## METHODS

From February 1973 through July 1974, *Helisoma* specimens from a Warm Station and a Cold Station in the littoral zone of Par Pond were routinely collected for oxygen consumption measurements. Due to the patchy distribution of snails in the wading zone (up to approximately one meter depth) and time restrictions, randomized sampling was undesirable for routine purposes. Preliminary experiments showed that the variance associated with the mean  $\text{O}_2$  consumption of snails collected arbitrarily was not different from that of snails collected in a paired, stratified, field-sampling scheme within the same station boundaries. Consequently, nonrandom dip netting was adopted for bimonthly collections from the two stations. After collection, snails were placed in insulated containers and immediately transported to the laboratory.

Maximum diameters were measured by gently rotating each snail around the axis of its spire within a standard micrometer caliper. Sampling was limited to adult snails (those with maximum outer diameter greater than 5 mm and dry weight greater than 0.01 g) because young snails showed much higher, more variable, and more size-

dependent O<sub>2</sub> consumption rates even when expressed on a weight specific basis. (A more-detailed discussion of the size factor will be presented later in this paper.)

A pair of Gilson\* differential respirometers (Model #GRP20) was used to measure the oxygen consumption of the snails immediately after bringing them to the lab. One of the respirometers was initially set at the collection temperature of surface water at the Cold Station; the other was similarly set at the Warm Station surface temperature. Such temperatures were generally within  $\pm 2^{\circ}\text{C}$  of the water temperature at the time and location of collection of experimental animals.

Twenty snails were randomly selected from each station's sample. The Cold Station subsample frequently incorporated both species. The relative number from each species varied between samples. Except on two or three occasions involving one or two individuals, the Warm Station samples consisted only of *H. trivolvis*.

The snails were individually placed in 15-mL-capacity reaction flasks containing 5 mL of autoclaved sand and 8 mL of centrifuged pond water. Although some snails tended to burrow more than others, no significant difference between O<sub>2</sub> consumption in the presence or absence of sand could be demonstrated in preliminary tests ( $P > 0.05$ ) and the incubation of sand alone caused no measurable O<sub>2</sub> consumption either. One ml of 20% KOH was placed in the side arm of each flask to absorb the CO<sub>2</sub> generated. Snails from the two stations were equally divided between the respirometers at the two field temperatures. The respirometer chambers were left open to the atmosphere

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\* Manufactured by Gilson Medical Electronics Inc., P.O. Box 27, Middleton, WI 53562.



while being shaken in a water bath for an hour of equilibration. Following equilibration, the chambers were sealed off from the atmosphere, and the first half-hour measurement interval was begun.

Special experiments were performed to evaluate the influence of acclimation on respiration and the influence of acute temperature depressions on respiration. The former experiments deviated from the routine procedure: Half of the Warm Station and Cold Station samples were collected in advance and acclimated in the lab for 48 hours at a constant temperature near that of the habitat. Additional snails were collected and acclimated for 48 hours at 5°C and 10°C above ambient. Subsequently, the oxygen consumption of the acclimated animals along with that of the nonacclimated snails (collected immediately before performing the experiment) was measured by the usual procedure. Experiments evaluating temperature depression responses were also performed. Temperatures were lowered from the field temperature and the respiration was measured at 5°C decrements.

Calculations of oxygen consumption followed instructions in the manufacturer's operation manual for the Gilson respirometer and in Umbreit, Burris, and Stauffer (1957). The final O<sub>2</sub> consumption rates were reported in microliters of oxygen per gram of total dry weight of snail per hour. Replicate measurements for each individual were averaged giving a single estimate of O<sub>2</sub> consumption for each organism. Subsequently, the means of these averages for individuals at each temperature were used to show:

- 1) the dependence of O<sub>2</sub> consumption on field temperature as it varies seasonally; and
- 2) the effect of acute temperature elevations on the O<sub>2</sub> consumption-temperature relation expressed in 1) above.

## RESULTS

### Metabolic Rates

The O<sub>2</sub> consumption of two species of *Helisoma* found in two temperature environments of the same lake has been measured at a series of field temperatures during an annual cycle. Figure 2 summarizes these measurements and the daily integral field temperatures for several intervals during the experimental period. The O<sub>2</sub> consumption for both species consistently decreased between October and April, the winter season. The oxygen consumption for both species tended to follow the field temperature. Relative rates for species and station differed by season (Table 1). *H. anceps* had the highest average rate in summer but the lowest rate in winter. Warm Station *H. trivolvis* had the highest rate in winter, but in summer its oxygen consumption was not significantly different from that of *H. anceps*. On an annual average rate basis, Warm Station *H. trivolvis* had a significantly higher oxygen consumption than the two populations of Cold Station snails which could not be distinguished statistically from one another.

When the above sets of O<sub>2</sub> consumption-rate estimates were plotted against the field temperatures at which they were made, interspecific

differences between regression lines describing the seasonal data became apparent (Figure 3a). The slope of the linear regression line plot for log O<sub>2</sub> consumption vs. temperature was 0.0159 for Warm Station *H. trivolvus*, 0.0121 for Cold Station *H. trivolvus*, and 0.0291 for Cold Station *H. anceps*. For both species and stations, these slopes were significantly different from zero ( $P < 0.025$ ). Even when the two species originated from the same station, the slope was significantly greater for *H. anceps* than for *H. trivolvus*. ( $P < 0.010$  for *H. anceps* vs. Warm Station *H. trivolvus* and  $P < 0.025$  for *H. anceps* vs. Cold Station *H. trivolvus*.) No difference between the slopes for the two populations of *H. trivolvus* was evident ( $P \geq 0.70$ ). Correlation coefficients for the three sets of data in Figure 3a were relatively low but highly significant ( $P = 0.0005$ ,  $P = 0.0005$ , and  $P = 0.0250$ ).

Evidence for seasonal acclimatization was found in the different O<sub>2</sub> consumption rates observed at the same field temperatures at different times of the year. For example, Table 2 compares some data excerpted from Figure 3a in which O<sub>2</sub> consumption was measured at the same temperature during a different season. Oxygen consumption was lower by a factor of 1.2 to 2.3 at the beginning of the winter and summer seasons than at the end of the seasons.

The dependence of oxygen consumption on body size could be detected by significant regressions (Table 3) in fewer than one-half the runs (38% for Warm Station *H. anceps*, 47% for Cold Station *H. trivolvus*, and 48% for Warm Station *H. trivolvus*).

To see if the elimination of size as a source of variation in the rate-temperature analyses affected the resulting regressions, a comparison of two methods of deriving values for the rate-temperature regressions was made. The first method, which has already been described, will be referred to as the Means Method, because the average O<sub>2</sub> consumption rates for the entire sample, irrespective of size, were incorporated into the regression. The second method (Weight Regression Method) derives its O<sub>2</sub> consumption values for the rate-temperature regression from O<sub>2</sub> consumption weight regression at specific temperatures.\* Only in experiments which produced significant ( $P \leq 0.05$ ) slopes, were weight regression results used (Table 3).

Oxygen consumption weight regressions were obtained for two specific weights: a small snail (30 mg) and an average size snail (62 mg). A least-squares prediction for respiration of snails of these two sizes at a given temperature was made from the O<sub>2</sub> consumption regressions. These predicted rates were plotted against temperature in Figure 4. Table 3 compares the curves derived by Weight Regression Method (Figure 4) with those derived by the Means Method (Figure 3a).

At field temperatures, the rate-temperature curves derived by the Weight Regression Method at 62 mg are not significantly different from the rate-temperature curves derived by the Means Method (Table 3). The correlation coefficients are likewise not improved. Thus, the scatter in Figure 3a is not appreciably reduced by examining only the

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\* Weights used in calculating all values are whole body dry weights.

average-size (62 mg) organism. Even among the small animals (30 mg), the slopes and the predictability of the equations do not change.

Acute temperature elevation experiments revealed different patterns of response for the two species of snails. The R-T curves for *H. trivolvis* showed progressively greater clockwise rotation with increasing  $\Delta T$ , whereas those for *H. anceps* remained statistically identical below 15°C  $\Delta T$  (Figure 3). Because of the reduced number of survivors at these temperature elevations, the exact shapes of the R-T curves for  $\Delta T = 15^\circ\text{C}$  are in question, but there is no doubt that their slopes are negative. Both species of *Helisoma* exhibited high mortality at  $\Delta T$ 's of 15°C, and the survival of *H. anceps* was poorer than that of *H. trivolvis*. Slopes of R-T curves for *H. anceps* did not differ significantly between stations for any temperature elevation below 15°C.

Both *H. anceps* and *H. trivolvis* show variable temperature coefficients ( $Q_{10}$ ) which are smaller than the value of 2 commonly reported in the literature. The average annual  $Q_{10}$  between field and 5°C above field temperature were  $1.02 \pm 0.14$ ,  $1.50 \pm 0.36$ , and  $1.52 \pm 0.16$  for *H. anceps*, Warm Station *H. trivolvis*, and Cold Station *H. trivolvis*, respectively. The coefficients of variation among individuals for a given temperature ranged between 295% and 14%. The temperature coefficients were even smaller for the 10°C than for 5°C elevations. In many cases the values reflected decreases in respiration.

In several special experiments, we tested the differences between R-T curves generated from acclimated vs. nonacclimated (field acclima-

tized) snails. Temperature coefficients,  $Q_{10}$ , computed for the three dates, are presented in Table 5. In all cases for both species and both stations, acclimated snails gave  $Q_{10}$  of almost double those for nonacclimated equivalents. A closer examination of the data indicates that low temperature rates were lower for acclimated than for nonacclimated animals and high temperature rates were higher.

#### DISCUSSION AND CONCLUSIONS

In general, our data support the idea that the exclusion of *H. anceps* from the warm arm of Par Pond is due to the elevated temperatures. The annual  $O_2$  consumption measured for *H. anceps* was similar at the Cold Station to that for *H. trivolvis* but most indications are that if *H. anceps* were living at the Warm Station it would have a higher metabolic demand than *H. trivolvis* resident there. Using the R-T curve for *H. anceps* (Figure 3) and the observed average temperature at the Warm Station, the average annual  $O_2$  consumption for *H. anceps* would be predicted to be 362  $\mu L O_2$  per gram per hour as compared with 341  $\mu L$  for *H. trivolvis* (Table 2). The general pattern of response to temperature appears to be much sharper and more rigid for *H. anceps* than for *H. trivolvis*. Not only is the R-T curve insensitive to acute temperature elevations (Figure 3), but acclimatization (Table 2) accounts for relatively smaller differences for *H. anceps* than for *H. trivolvis*. *H. anceps*'s metabolism tends to follow field temperature more directly than that of *H. trivolvis*. Some littoral areas inhabited by these snails may fluctuate as much as  $10^\circ C$  during the course of a single day. The ability to reduce oxygen

consumption during such excursions would tend to conserve energy reserves. Under conditions involving acute  $\Delta T$ 's of 5°C and above, *H. trivolvis* appears to reduce its metabolism to levels below those at regular field temperatures. *H. anceps* shows no such metabolic adjustment and may be at a disadvantage in any competition with *H. trivolvis*. Wieser (1973) discusses the possibility that respiratory plateaus may be related to limited supplies of substrates such as ADP. An examination of the energy charge (Holm-Hansen and Booth, 1966) condition of the two species of *Helisoma* in relation to temperature would be instructive.

It is conventional to construct R-T curves from the results of short-term experiments with laboratory snails acclimated to constant temperatures. This sort of experiment speaks to the question of physiological potential but not to that of ecological response. The ecological questions relate to what happens in the natural system as temperature changes seasonally and in cooling systems with changes in power plant operations. Since they reflect field conditions, the graphs in Figure 3 are ecological R-T curves. Sheanon and Trama (1972) using *H. trivolvis* from the Raritan River, New Jersey, presented physiological R-T curves for laboratory-held animals acclimated 24 hours. After converting their data to a total weight basis (using their figure of 28% for tissue weight as a fraction of total), the relationship for log O<sub>2</sub> consumption became  $\log R = 0.032\% + 1.946$  which appears to be steeper than our ecological R-T curves. The difference evidently lies in the fact that acclimated snails tend to give

steeper responses. Temperature coefficients computed for data derived from the Sheanon-Trama curve are 1.75 times as great as the temperature coefficients determined similarly from our R-T curve. Close agreement was obtained from the special experiments set up to distinguish the effects of acclimation (Table 5). We calculated that the average  $Q_{10}$  for acclimated Cold Station *H. trivolvis* is 1.7 times the  $Q_{10}$  for nonacclimated animals.

The failure to consistently detect the expected inverse relation of oxygen consumption to body size is unexplained. Data were examined to determine whether significant regressions appeared to be associated with wider ranges of body size, to particular patterns of thermal history, to the occurrence of locomotor activity or to the specific ranges of temperatures employed. None of these factors appeared to account for the observed variability which overwhelmed the size effect. As described earlier, the trends in R-T curves remained unchanged for small and average sized animals. Therefore, we believe the trends fairly represent the responses of the experimental snails.

Our data show that the *H. trivolvis* population in the warm arm would experience the increase in metabolic requirement conjectured to be one outcome of the exposure of ectothermic organisms to thermal effluents. Assuming that oxygen consumption reflects metabolic demand and that the entire population was exposed to the hyperthermal effluent, *H. trivolvis* would require about 20% more energy to maintain itself at the Warm Station than under ambient conditions (Table 1). The segment of the total population actually subjected to such a



metabolic increase in the warm arm is difficult to estimate because the thermal plume is variable in horizontal extent and the population is mobile and patchy. Interestingly, Wood (1976) could not demonstrate any consistent differences in growth rate for *H. trivolvus* between thermal and nonthermal sites. Neither he nor we could demonstrate a significant difference in standing crop between areas. *H. trivolvus* may be able to avoid the thermal plume to some extent by behavioral responses and can, as we have demonstrated, regulate this physiological response to exposure to elevated temperatures, but the overall impression is that it does experience some metabolic increase which must be offset by compensatory increases in total energy intake and utilization.

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TABLE 1

Mean Oxygen Consumption for *Helisoma* from  
Different Locations,  $\mu\text{L O}_2/(\text{g})(\text{hr})$

Snail	Warm Station		Cold Station		
	<i>H. trivolvis</i>	<i>H. anceps</i>	<i>H. trivolvis</i>	<i>H. trivolvis</i>	
$\bar{R} \pm \text{SE}$	341 $\pm$ 9	297 $\pm$ 21	285 $\pm$ 14	285 $\pm$ 14	Annual
n	280	78	113	113	
CV =	44.2	62.4	52.2	52.2	
$\bar{R} \pm \text{SE}$	275 $\pm$ 15	135 $\pm$ 15	229 $\pm$ 17	229 $\pm$ 17	Winter
n	77	77	32	32	
CV =	47.9	97.5	42.0	42.0	
$\bar{R} \pm \text{SE}$	366 $\pm$ 10	274 $\pm$ 24	307 $\pm$ 18	307 $\pm$ 18	Summer
n	203	53	81	81	
CV =	38.9	63.8	52.8	52.8	

TABLE 2

Effect of Seasonal Acclimatization on Snail O<sub>2</sub> Consumption

Station	Species	Field Temperature, °C	Month	Respiration, μL O <sub>2</sub> /(g) (hr)
Cold	<i>H. trivolvis</i>	29	June	282 ± 26
			August	447 ± 107
Cold	<i>H. trivolvis</i>	17.5	November	130 ± 17
			March	298 ± 36
Cold	<i>H. anceps</i>	17.5	November	137 ± 18
			March	233 ± 58
Warm	<i>H. trivolvis</i>	22.5	May	246 ± 64
			November	328 ± 17
Warm	<i>H. trivolvis</i>	35.0	June	460 ± 50
			August	576 ± 38

TABLE 3

Regression of Respiration on Body Weight in *Helisoma*

Species and Station	Temperature, °C	Number Individuals in Sample	Correlation Coefficient	Slope of Regression $\log y = m(\log x) + b$	Y Intercept
<i>H. trivolvis</i>	18.5	9	-0.7132 <sup>a</sup>	-0.5209 <sup>a</sup>	3.3728
Warm Station	19.0	10	-0.8693 <sup>b</sup>	-0.7118 <sup>b</sup>	3.5505
	22.5	10	-0.6302 <sup>a</sup>	-0.2546 <sup>a</sup>	3.0231
	24.0	10	-0.6621 <sup>a</sup>	-0.5793 <sup>a</sup>	3.5912
	27.5	10	-0.7218 <sup>a</sup>	-0.4778 <sup>a</sup>	3.5215
	29.0	10	-0.8831 <sup>b</sup>	-0.5350 <sup>b</sup>	3.5433
	29.8	9	-0.8985 <sup>b</sup>	-0.5641 <sup>b</sup>	3.6809
	30.0	10	-0.7009 <sup>a</sup>	-0.3646 <sup>a</sup>	3.1307
	30.5	10	-0.6617 <sup>a</sup>	-0.4720 <sup>a</sup>	3.3274
	32.5	10	-0.7243 <sup>a</sup>	-0.7191 <sup>a</sup>	3.7924
	33.5	10	-0.7884 <sup>b</sup>	-0.4258 <sup>b</sup>	3.3804
	34.8	10	-0.6478 <sup>a</sup>	-0.2315 <sup>a</sup>	3.1023
	35.0	10	-0.7219 <sup>a</sup>	-0.4634 <sup>a</sup>	3.5075
<i>H. anceps</i>	14.0	5	-0.9296 <sup>a</sup>	-1.6794 <sup>a</sup>	5.1194
Cold Station	27.0	8	-0.7303 <sup>a</sup>	-0.4866 <sup>a</sup>	3.2498
	29.0	6	-0.8290 <sup>a</sup>	-0.6204 <sup>a</sup>	3.7993
	30.0	7	-0.8479 <sup>a</sup>	-0.4609 <sup>a</sup>	3.3403
	30.0	9	-0.7718 <sup>a</sup>	-0.5874 <sup>a</sup>	3.5134
<i>H. trivolvis</i>	17.5	6	-0.8872 <sup>a</sup>	-0.5017 <sup>a</sup>	3.2776
Cold Station	23.0	6	-0.9168 <sup>a</sup>	-0.4803 <sup>b</sup>	3.1811
	26.5	10	-0.8723 <sup>b</sup>	-0.5359 <sup>b</sup>	3.5481
	28.0	4	-0.8655 <sup>a</sup>	-0.7069 <sup>a</sup>	3.8268
	29.5	6	-0.9216 <sup>b</sup>	-0.6781 <sup>b</sup>	3.7924
	30.0	3	-0.9992 <sup>a</sup>	-0.2789 <sup>a</sup>	2.0241
	30.0	9	-0.8630 <sup>a</sup>	-0.4241 <sup>a</sup>	3.1818

a. Significant at  $P = 0.05$ .

b. Significant at  $P = 0.01$ .

c. Only results giving slopes significantly different from zero have been included.

TABLE 4

Comparison of Two Methods of Deriving Metabolism-Temperature Relations

Station	Species	<u>Means Method</u>			<u>Weight Regression Method</u>			<u>Two-Tailed Tests</u>		
		Temp. Range	Slope	Intercept	Temp. Range	Slope	Intercept	t	df	P
Warm	<i>H. trivolvus</i>	18.0- 35.0°C	0.0159 ±0.0039	2.0896	18.5- 35.0°C	0.0140	2.1593	0.4896	25	>0.5
Cold	<i>H. trivolvus</i>	13.0- 30.0°C	0.0121 ±0.0029	2.1367	17.5- 30.0°C	0.0143	2.1057	0.4702	16	>0.5
Cold	<i>H. anceps</i>	13.0- 30.0°C	0.0291 ±0.0078	1.7209	14.0- 30.0°C	0.0270	1.7270	0.3441	12	>0.5

TABLE 5

Effect of Acclimation on  $Q_{10}$ 

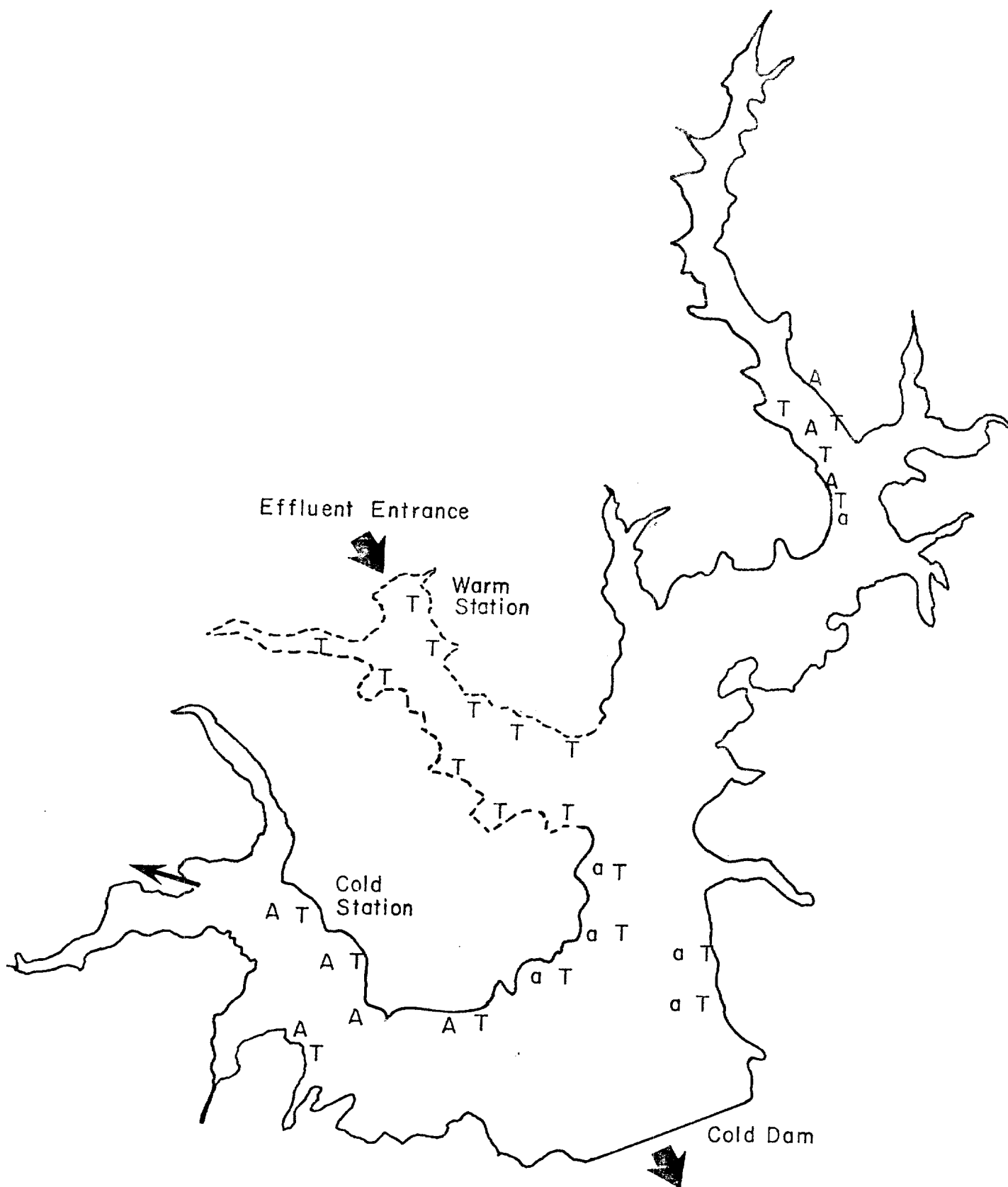
Date	Station	Species	Temperature Range	$Q_{10}$	
				Acclimated	Nonacclimated
4/24/74	Warm	<i>H. trivolvus</i>	20-30°C	1.7	1.0
9/11/74	Warm	<i>H. trivolvus</i>	25-35°C	1.1	0.9
10/9/74	Warm	<i>H. trivolvus</i>	25-35°C	1.8	0.5
4/24/74	Cold	<i>H. trivolvus</i>	20-30°C	1.6	1.0
9/11/74	Cold	<i>H. trivolvus</i>	25-35°C	1.6	1.1
10/9/74	Cold	<i>H. trivolvus</i>	25-35°C	1.7	0.7
9/11/74	Cold	<i>H. anceps</i>	25-35°C	1.3	0.9
10/9/74	Cold	<i>H. anceps</i>	25-35°C	1.8	0.8

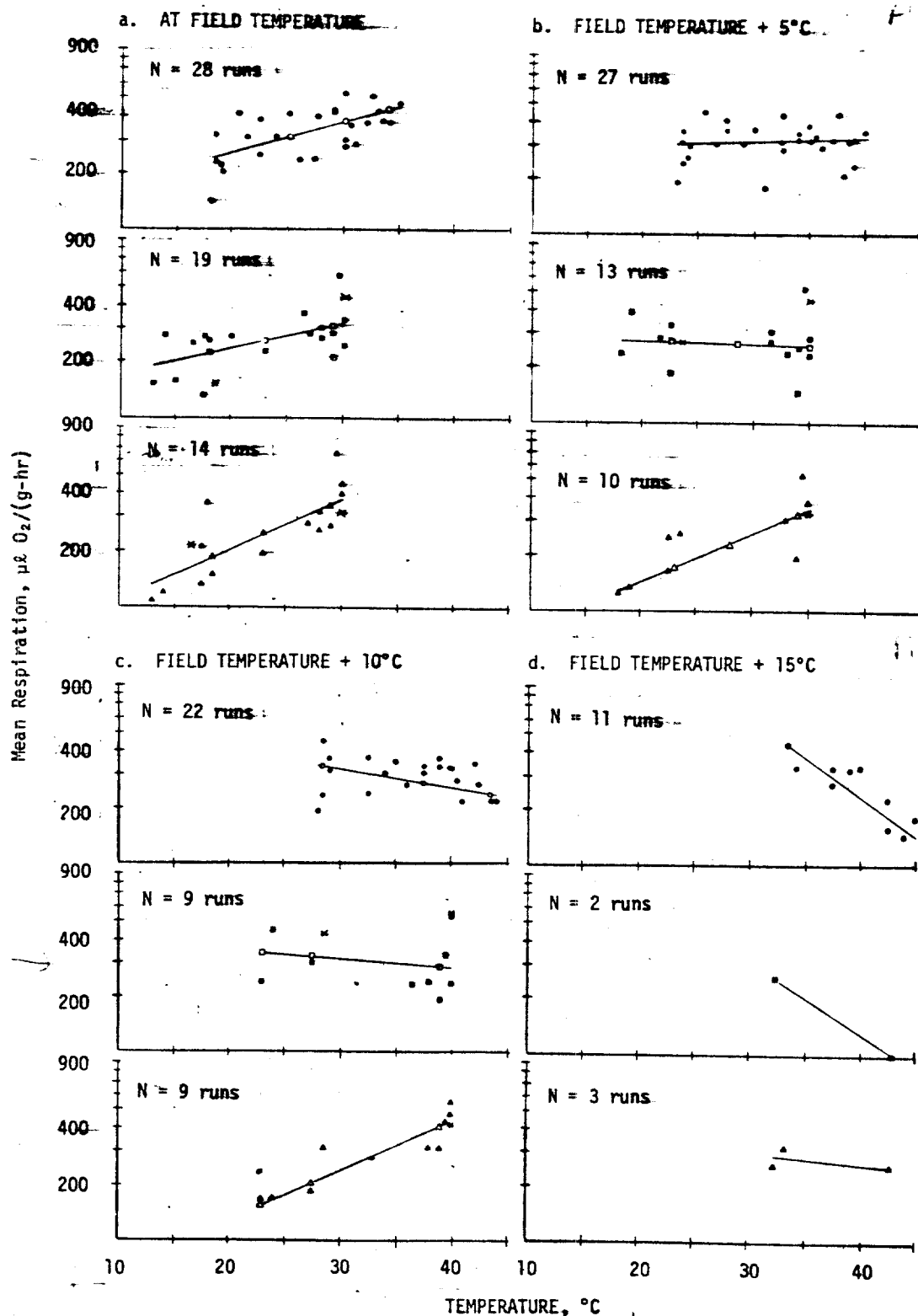


FIGURE 1. Par Pond, Showing Snail Distribution, Thermal Regions,  
and Sampling Stations

FIGURE 2. Field Temperature and Oxygen Consumption Cycles for  
*Helisoma* from Par Pond

FIGURE 3. Dependence of Respiration on Temperature in  
*Helisoma* (Means Method)





Open symbols are linear least-squares predicted values.

Solid symbols are observed values.

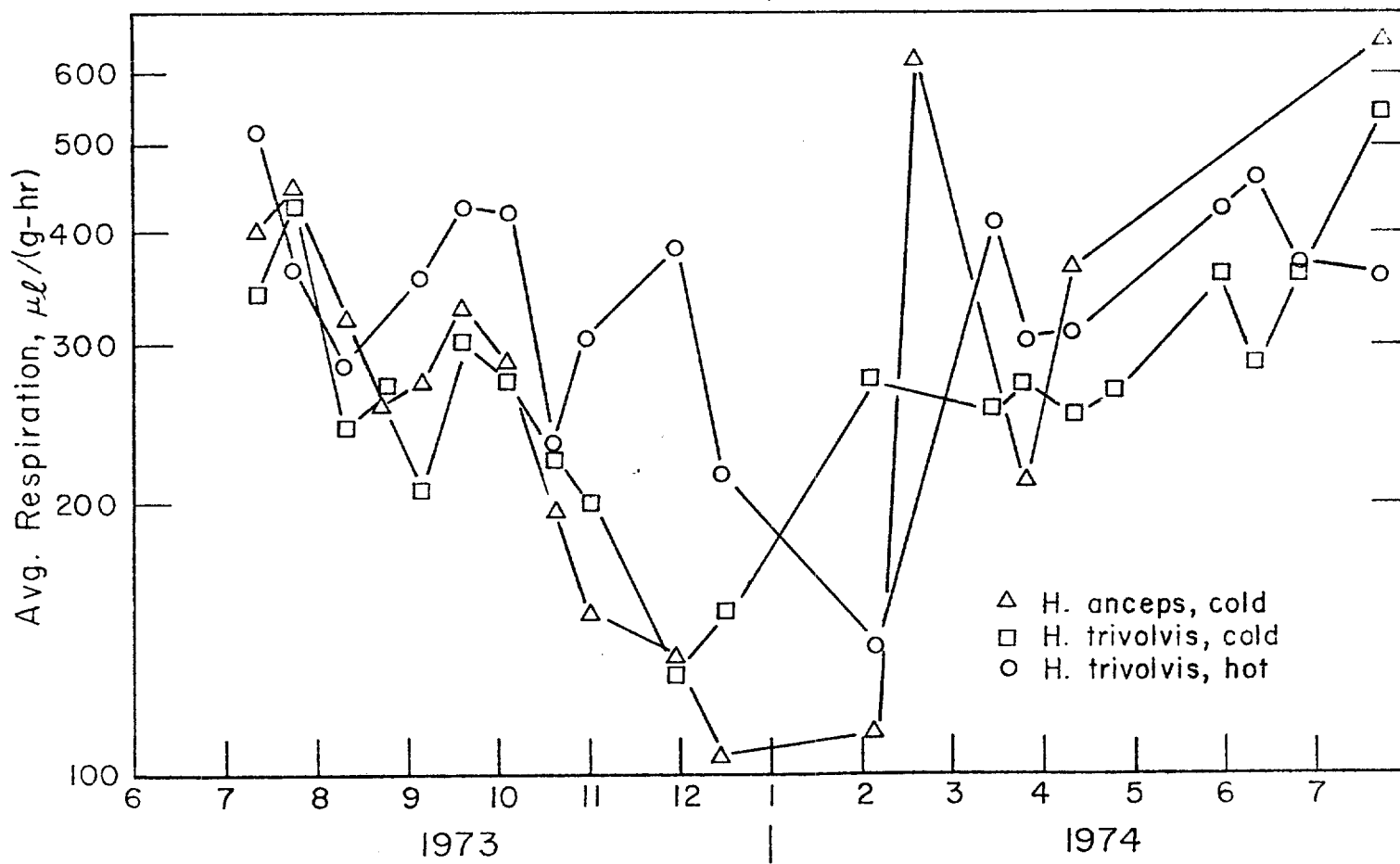
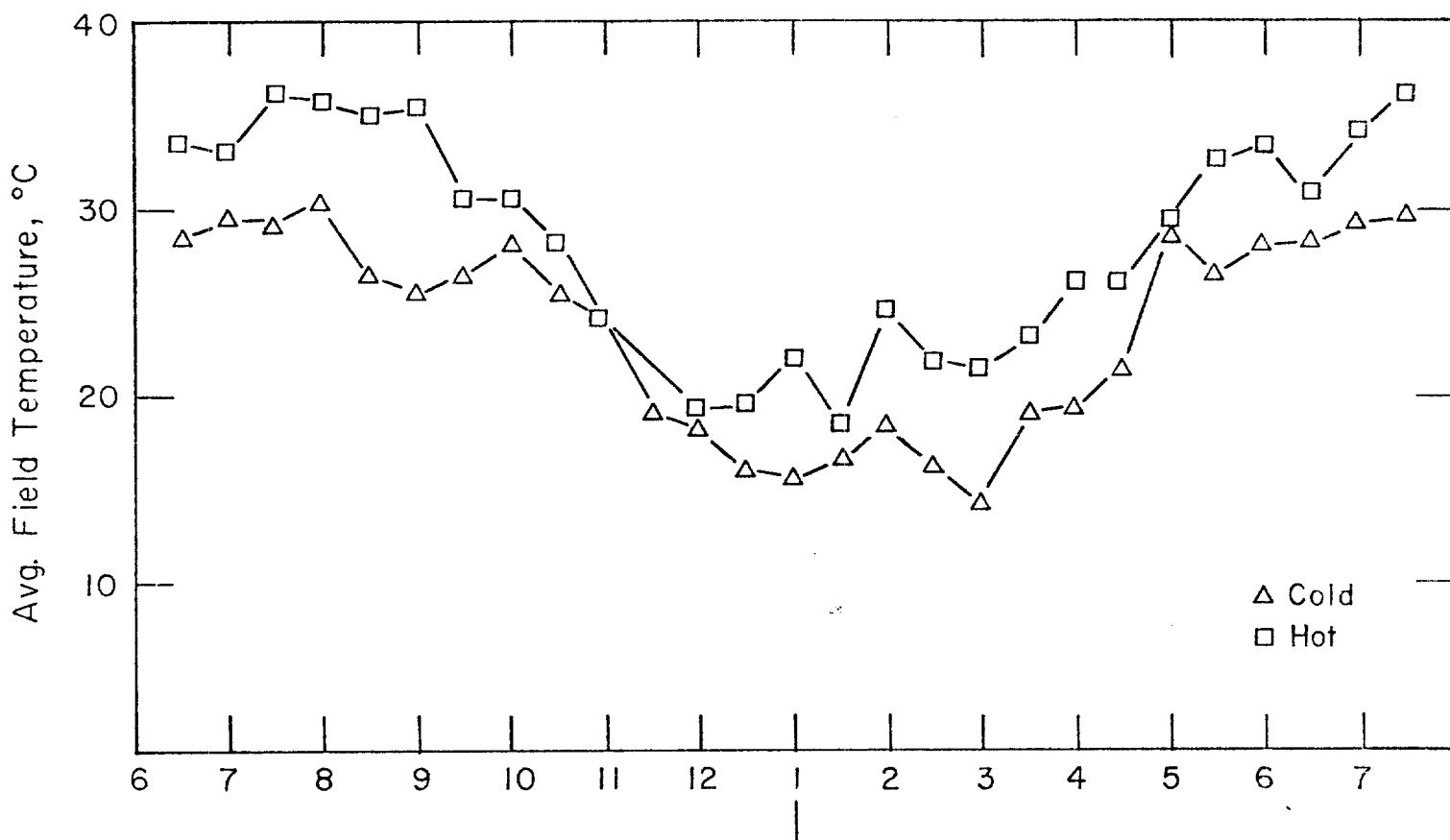
\* N = 1 for that run.

○ Warm Station *H. trivoltis*.

□ Cold Station *H. trivoltis*.

△ Cold Station *H. anceps*.

(25)



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